

BEAUFORTIA

BULLETIN ZOOLOGICAL MUSEUM

UNIVERSITY OF AMSTERDAM

Vol. 50, no. 2

November 3, 2000

A NEW APPENDICULARIAN, *OIKOPLEURA GORSKYI* N. SP. (TUNICATA), FROM NORWEGIAN FJORDS

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Key words: Urochordata, Appendicularia, Oikopleuridae, *Oikopleura gorskyi*

ABSTRACT

A new appendicularian, *Oikopleura gorskyi* n. sp., recovered from numerous plankton samples taken at depths between 1200 and 400 m in Sognefjorden, western Norway, as well as in more shallow water in this and other western Norwegian fjords, is described. The species is easily identified by the limited extension of its oikoblastic epithelium, the small size of its right stomach lobe and the disposition of its subchordal cells in two segments of an antero-posterior line with some 13 and 8 plate-shaped cells respectively. The unique pattern of its house rudiment inclusion body and the unique cell nuclear pattern in its oikoblastic epithelium are additional, although less easily observable, characters of this species.

INTRODUCTION

As part of the first international research project on planktonic Appendicularia (EURAPP: The impact of appendicularians in European Marine Ecosystems, MAS-3-C98-0161) vertically split zooplankton samples have been taken at monthly intervals from near the bottom (1200 m) to the surface at a station in Sognefjorden, western Norway, during the period March 1999 - February 2000. As far as we know a comparable sampling program has never been conducted before in this deepest (max. depth 1308 m) and longest (approximately 200 km long) ice-excavated fjord on earth. The entrance sill to this fjord

from the North Sea is only 150-200 m deep.

In most of our plankton samples derived from 1200 to 400 m depth of this fjord, and more occasionally in shallower water of this and other fjords, we have isolated several specimens of a hitherto unknown oikopleurid appendicularian which will be described below.

MATERIALS AND METHODS

Vertically split zooplankton samples were made from R/V 'Hans Brattström' at a station in Sognefjorden, (61°03'50"N 05°22'00"E, bottom depth 1250 m), and from R/V 'Fritillaria' in Herdlefjorden (60°32'50"N 5°01'30"E, bottom

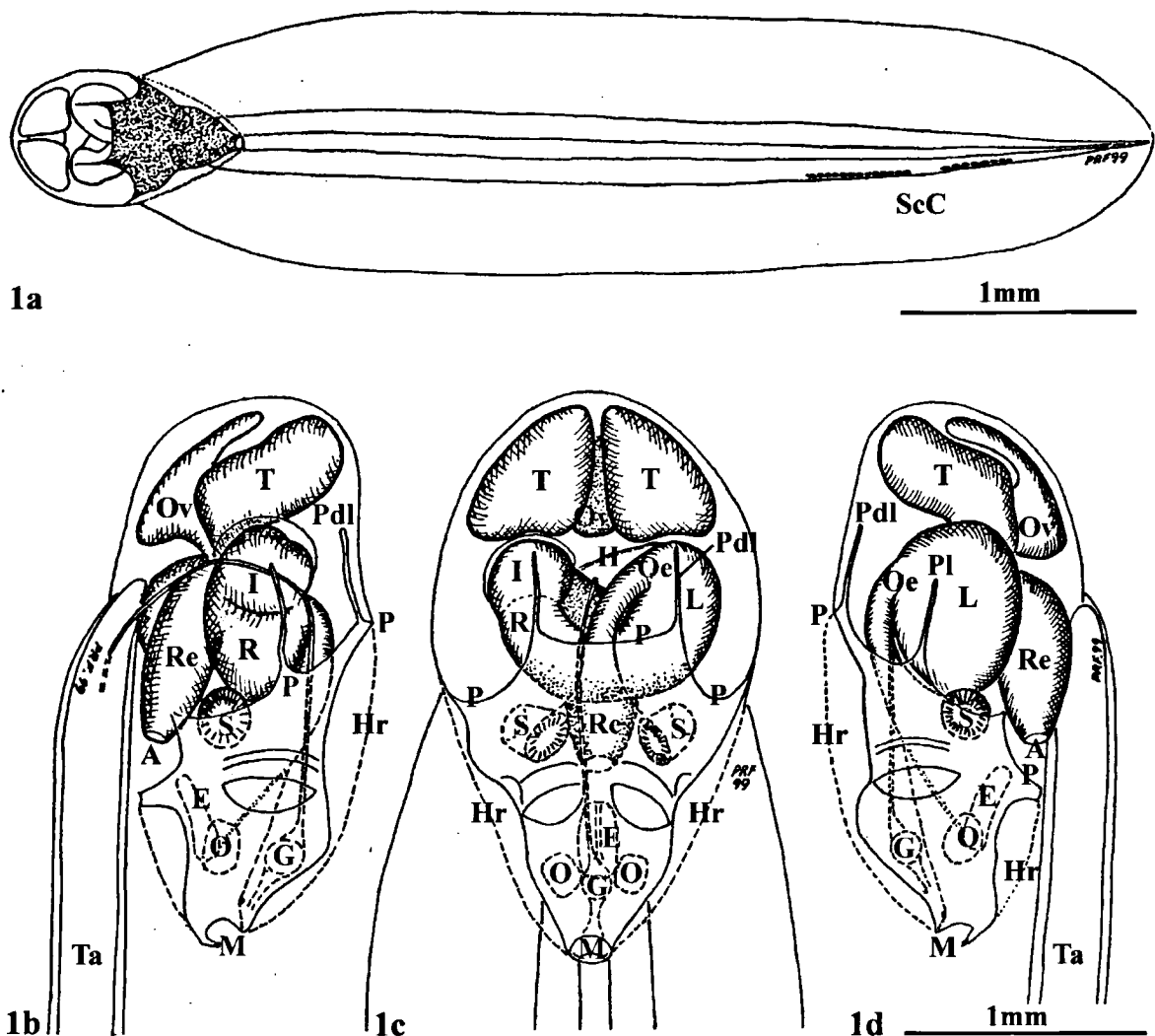


Fig. 1. *Oikopleura gorskyi* n. sp. A, line drawing of entire animal. Note the limited extension of the oikoblastic epithelium (stippled) relative to the position of the digestive tract and gonads, and the presence of some 20 subchordal cells (ScS) in an interrupted line in the posterior 1/3 of the tail. B-D, line drawings of the trunk as seen from the right (B), dorsal (C) and left (D) side. A, anus. E, endostyle. G, cerebral ganglion. H, heart. Hr, house rudiment. I, intestine. L, left stomach lobe. M = mouth. O, oral gland. Oe, oesophagus. Ov, ovary. P, posterior border of oikoblastic epithelium. Pdl and Pl, dorso-lateral and lateral strands of oikoblastic epithelium. R, right stomach lobe. S, spiracles. Re, rectum. T, testis. Ta, tail.

depth 270 m), north of Bergen. The vertical hauls were made at low speed (1/4 to 1/2 knot) with a 57 cm diameter closing net of 90 mm pore size, fitted with a 2L sample container with filter windows in its upper part. (The overall geometry of the net equalled that of a standard working panel 2 (WP2) net as described in Fraser, 1968. The depth intervals sampled in Sognefjorden were 1200 to 800 m, 800 to 400 m, 400 m to thermocline (variable between 60 and 30 m), and ter-

mocline to surface. Occasionally, the deepest interval was split in two hauls 1200 to 1000 m and 1000 to 800 m. In Herdlefjorden unsplit vertical samples were made from bottom to the surface. Simultaneous vertical profiles of temperature, salinity and oxygen were logged by a MiniSTD/CTD model SD204 from SAIV A/S, Bergen.

As soon as the samples arrived on deck the content of the bucket was either examined under a

stereomicroscope (Olympus SZX-12) in dark field illumination and the observed appendicularians pipetted, with as little as possible of its surrounding water, into a bowl of filtered seawater (0.2 mm) or directly into a fixative consisting of 4% formaldehyde (depolymerized from paraformaldehyde), 40 mM sodium cacodylate at pH 8.0 and approximately 60% filtered (0.2 mm) seawater. Alternatively, the entire plankton container was emptied into a glutaraldehyde and sodium borate concentrate which upon dilution by the sample reached a final concentration of ~0.5% glutaraldehyde, ~0.5% sodium borate and ~60% seawater.

Live and fixed appendicularians were examined and photographed under stereo- and compound microscopes (Olympus SZX-12, respectively Olympus IX and Nikon Labophot) either onboard or after returning to a landbased laboratory. Live specimens were photographed without further treatment, whereas fixed samples were photographed after partial clearing in 60 to 80% glycerol, after staining with a variety of histological stains, including the DNA-specific fluorochrome DAPI (4', 6-diamidino-2-phenylindole-HCl) (Sigma) (Porter and Feig, 1980) and/or after various microdissectional approaches.

Bioluminescence was recorded in a luminometer equipped with a photomultiplier tube and built according to specifications from Dr J. Blinks, Friday Harbor laboratories, University of Washington.

DESCRIPTION

Oikopleura gorskyi n. sp.

Figs. 1-4

MATERIAL. - Holotype: deposited at the Institute of Biodiversity and Ecosystem Dynamics (Zoologisch Museum), University of Amsterdam (# ZMA. Tu. 5461). Type locality: Sognefjorden, western Norway (61°03'50"N 05°22'00"E, bottom depth 1250 m). Date: 5 July 1999. Depth: 400-35 m vertical tow. Salinity: 3.528-3.317‰, Temperature: 7.11-7.75°C. Collector type: plankton net with 90 µm pore size.

Preservative: fixed immediately in 4% formaldehyde (depolymerized from paraformaldehyde) in 40 mM sodium cacodylate and 60% filtered seawater (pH 7.8). After one year transferred to 0.5% glutaraldehyde in 2% sodium borate and 60% seawater (pH 7.8).

Size of holotype: total trunk length: 1.250 mm. Trunk

length without gonad: 1.0 mm. Maximum trunk width: 0.66 mm. Maximum trunk height: 0.56 mm. Tail length: 5.8 mm. Notochord width: 0.16 mm. Maximum muscle band height (dorso-ventral): 0.36 mm. Maximum tail width (incl. fins): 0.76 mm.

REMARKS. - The new species was recovered in low or moderate numbers from most of the deep plankton tows in Sognefjorden and from approximately half the tows in Herdlefjorden. In the latter fjord, which was sampled at weekly intervals throughout a year, the total catch approached 100 specimens. The description below is based on several well preserved specimens and the holotype was chosen among those which demonstrated the characteristic features in the most convincing way.

DESCRIPTION. - The new species confines to the general morphology of oikopleurid Appendicularia and may, for descriptive purposes, be subdivided in a pearshaped trunk and a flattened, retroflexed tail. These, and some of its species-specific details, are described below under separate headings.

Trunk: the trunk is pearshaped with a narrow and conical pharyngeal (anterior) segment and a wider, roundish, digestive and gonadal (posterior) segment (Figs. 1 and 2A-C). The trunk size is approximately 1 mm in length, 0.6 mm in width and 0.5 mm in height in the largest specimens found. The sexual maturity of these corresponded to stage 4 on the scale defined by Shiga (1976) for *O. labradoriensis* Lohmann, 1892. The widest and highest portion of the trunk in the transverse plane is at the level the posterior border of the dorsal oikoblastic epithelium or the middle part of the digestive segment.

Mouth: the mouth is apical, almost circular with a diameter of approximately 100 µm. It is equipped with a prominent lower lip on which rim a few rows of short stereocilia is present (Fig. 1D).

Oral cavity and pharynx: the oral cavity is short and opens posteriorly into a pharyngeal cavity of increasing diameter and height. The bilateral circular ciliated rings of the spiracles defines the postero-lateral corners of the floor of this cavity. In the anterior part of the floor, bilateral, large oral glands, about 100 µm in diameter, are present (Figs. 1B-D, 2A-C). These are uni-

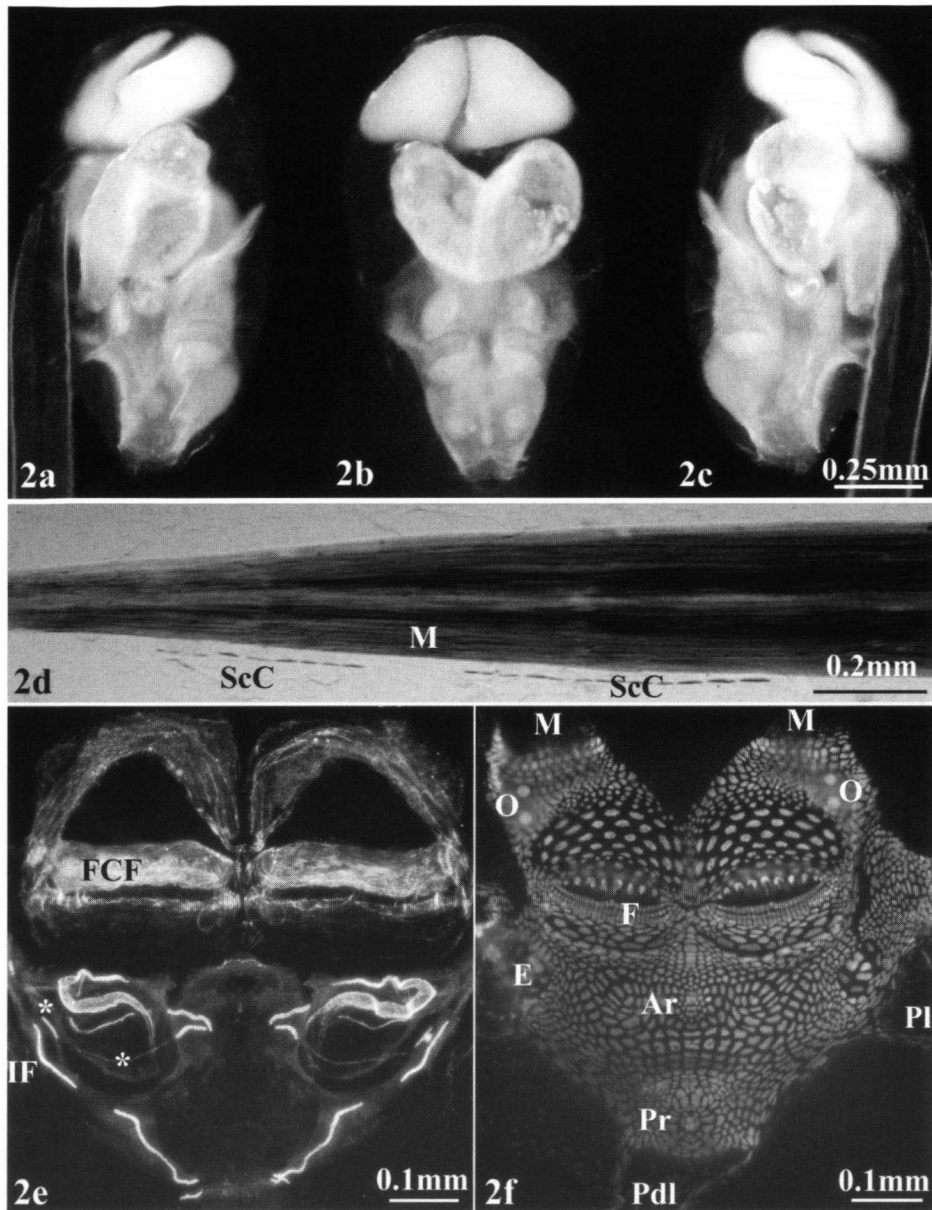


Fig. 2. *Oikopleura gorskyi* n.sp. A-C, microphotographs of the same trunks in the same directions as shown in Figs. 1B-D. D, micrograph of the posterior tail segment, as seen from the right side, with its subchordal cells squeezed ventrally below the margin of the tail musculature (M). E, dark field micrograph of house rudiment, microdissected from the trunk of an animal with trunk length > 900 mm, cut open and unfolded before mounting for microscopy. A unique, bilateral pattern of 7 inclusion body lines (white lines) is seen behind the food concentrating filter anlagen (FCF) and dorsal to the inlet filter anlagen (IF). Note that two of the lines have thin and faint middle segments (asterisks) and thicker segments at both ends. F, UV-fluorescence micrograph of DAPI-stained oikoblastic epithelium microdissected from the trunk of an animal with trunk length > 900 mm, cut open and unfolded before mounting for microscopy. Note the presence of bilateral Fol's (F), Eisen's (E) oikoplasts as well as an anterior (Ar) and posterior (Pr) rosette along the mid-dorsal line of the nuclear pattern, and the two spherical nuclei of the oral glands (O) superimposed on the oikoblastic cells near the mouth region (M). The dorso-lateral (Pdl) and lateral (Pl) strandwise extensions of the oikoblastic epithelium is also visible.

cellular glands, but each contains two spherical nuclei (Fig. 2F) and often reveals a pseudo-rectangular profile with rounded corners in lateral

and dorsal projection. Between these glands, from their posterior half and backwards, and filling the space between them, a wide and straight

endostyle is found (Fig. 1B-D). This terminates approximately 0.1 mm in front of the anal papilla and, based on fluorescence microscopy of DAPI stained microdissected specimens, consists of 2-4 large anterior cells and bilateral, antero-posterior rows of some 17 cells on both sides of a median furrow, in which ventral part a few elongated nuclei are present. The endostyle measures approximately 160x100x50 μm in length, width and height respectively. The lateral walls of the pharyngeal cavity curve dorsally towards the midline and merge in a narrow roof which gain height posteriorly where it joins the dorsal wall of the oesophagus. The bilateral peripharyngeal ciliated bands, originating at the anterior end of the endostyle, course towards the same junction, seemingly in a straight line when viewed in lateral projection (Fig. 1D).

Digestive tract: the ciliated oesophagus starts out as a funnel-shaped structure from the roof of the pharyngeal cavity and curves smoothly posteriorly as a cylindrical tube to join a voluminous left stomach lobe at its posterior dorso-medial pole (Figs. 1D, 2B-C). This lobe is almost circular in lateral projection and there is no real coecum behind the cardia. The left stomach lobe is somewhat compressed in the transverse plane and contains a prominent row of giant glandular cells in its wall along the posterior and ventral perimeter. The antero-medial wall of the left lobe communicates widely with a right stomach lobe which is smaller than the left one. It may conveniently be described as a short tubular structure, with a 90° bend in its central axis, from running in the transverse direction at the junction with the left lobe, to running posteriorly towards the intestine (Figs. 1C, 2A-B). The terminus of this tube is clearly demarcated from the proximal segment of an equally short intestine by a slight constriction (no real pylorus) and a change in the cellular pattern of its wall. The short intestinal segment, easily visible in dorsal projection and from the right side (Figs. 1B-C, 2A-B), courses ventrally and medially to continue into a rather voluminous and elongated rectum which courses anteriorly in the median plane to terminate in an anal papilla projecting from the ventral trunk surface, between and slightly anterior to, the external openings of the spiracle canals.

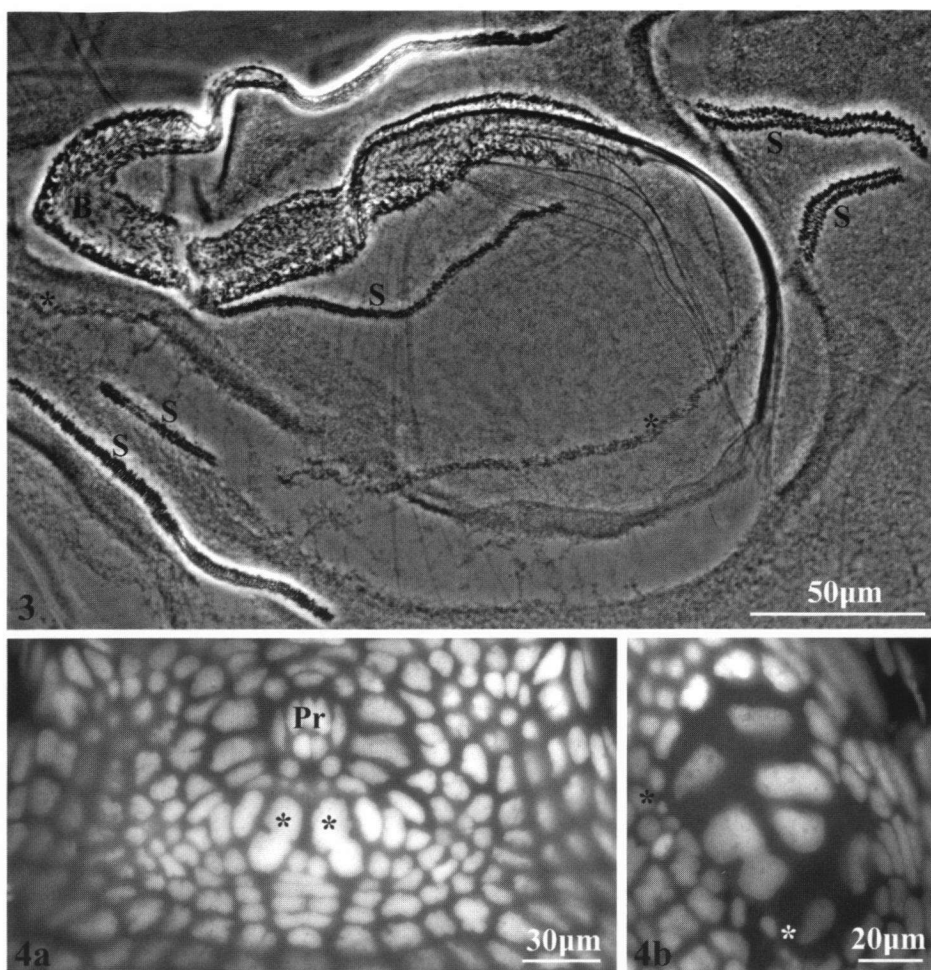
Gonads: these vary in size in distinct speci-

mens. In early stages of their differentiation only a small thickening of the otherwise thin and transparent posterior body wall is seen (maturity stage 2 of Shiga, 1976). Later, bilateral testes, of a curved sausage-shape, border a single median and less developed ovary (Shiga, 1976, stage 3). In the most mature specimens examined, the testes occupy a volume of approximately the same size as the stomach and gut segments, but is still located entirely posterior to the digestive structures (Shiga, 1976, stage 4) (Figs. 1 and 2). The ovary is still small at this stage of maturation.

Heart: this is visible in dorsal view of the trunk as a thin film spanning the cleft behind the two stomach lobes (Fig. 1C). A comparable thin film was seen around the intestinal segment in dorsal and right lateral view (Figs. 1B-C).

Nervous system: this includes a large spherical statocyst (approximately 0.1 mm in diameter) attached to the cerebral ganglion above the roof of the pharyngeal cavity at a transverse level corresponding to the oral glands (Fig. 1D). The main nerve trunk courses from this ganglion posteriorly to the right side of the oesophagus, to curve behind and between the two stomach lobes and the rectum to gain access to the dorsal (or left) side of the tail where it soon joins a main caudal ganglion.

Oikoblastic epithelium: the housebuilding epithelium covers only a small portion of the anterior trunk (Figs. 1 and 2). It extends from the mouth region to half way across the stomach in dorsal projection, but ends corresponding to the anterior margin of the stomach and rectum in lateral projection. At the ventral surface of the trunk it terminates at a prominent distance in front of the anus and also anterior to the posterior margin of the endostyle. Fol's and Eisen's oikoplasts may be identified on the dorso-lateral, respectively ventro-lateral surface of this epithelium. Further, a mid-dorsal anterior and a posterior rosette may be discerned on microdissected and mounted epithelia as seen in the fluorescence microscope after staining with the DNA-specific fluorochrome DAPI (Fig. 2F). The entire nuclear pattern is similar to the general pattern seen in most other oikopleurids, however, the Eisen oikoplasts are characterised by only 5-7 'Neben'-cells, whereas all other examined species have at least twice as many (Spriet, 1997; Spriet



Figs. 3-4. *Oikopleura gorskyi* n. sp. 3, high power phase contrast light micrograph of some of the inclusion bodies in a microdissected and unfolded house rudiment. Note the s-shaped wide band (B) with loosely packed lumisomes, as contrasted to the narrow double strands (S) with more densely packed lumisomes of somewhat variable size and shape. The thin middle segment between more voluminous terminal double strands are indicated by asterisks. 4A, UV-fluorescence micrograph of same specimen as shown in Fig. 2F, showing detail of A: the posterior dorsal oikoblastic epithelium, including the posterior rosette (Pr) and two enlarged cell nuclei just in front of this (asterisks). 4B, Eisen's oikoplast with its low number of 'neben'-cells (between asterisks).

and Flood, in prep.) Additionally, two large cell nuclei close to the mid-dorsal line, just anterior to the posterior rosette (Figs. 2F and 3) is unlike anything seen in comparable specimens from several other species of the subgenus *Vexillaria* Lohmann, 1933 of the *Oikopleura* Mertens, 1830 genus (Spriet and Flood, in prep.). Two long and slender dorso-lateral strands of oikoblastic cells, and two equally slender, but shorter lateral strands, project posteriorly from this margin to approach the gonadal segment of the trunk (Fig. 2F). A third set of short ventral extensions are present on the medial side of the external spira-

cle openings.

House rudiment and inclusion bodies: in a few well preserved specimens the secretory product of the oikoblastic epithelium could be dissected from the trunk as an acellular anlage or rudiment for the typical filter houses which these animals live inside. These house rudiments reveal the typical *Oikopleura* pattern; with 'Anlagen' for inlet- as well as food concentrating filters (Fig. 2E) and for a striated tail chamber. Most prominent and probably of highest diagnostic value for the new species is a unique pattern of inclusion body, dispersed over the dorso-

lateral surface behind the rudimentary food concentrating filters and dorsal to the rudimentary inlet filters. This bilateral pattern consists of seven lines of tightly packed, highly refractive and autofluorescent (and probably bioluminescent) bodies of 1 to 3mm diameter (cp. lumisomes as defined in Galt and Flood, 1998). The autofluorescence of fresh, unfixed lumisomes within these inclusion bodies was yellow-green when excited by blue light and blue when excited by UV light. The observed pattern of inclusion body (Fig. 2F) is unlike every pattern known from other species of *Oikopleura* and may be divided in a posterior group of one short and one long oblique line, and an antero-lateral group of 5 lines, two of which are characterized by having faint and narrow middle segments and wider dorsal and ventral segments (Fig. 3). Most lines appear to have their lumisomes, of somewhat variable size and shape, distributed on both sides of a narrow structureless core, giving the impression of a double line, as typically found in *O. parva* Lohmann, 1896 house rudiments (pers. obs.). The most anterior inclusion body is unusually wide and curved into a S-shaped structure. Its 'lumisomes' are less densely packed than in the other lines and the structure shows some resemblance to a comparable structure in house rudiments from *O. albicans* Leuckart, 1854 (pers. obs.).

Luminometer recordings from intact animals showed flash-like light emission in responses to mechanical stimulation comparable to that previously recorded from *O. labradoriensis* and *O. dioica* (Galt and Flood, 1998).

Epidermis: the epidermis beyond the oikoblastic zone is very thin and transparent, and curves smoothly around the digestive and gonadal segments of the trunk leaving considerable, seemingly empty, blood lacunae between these structures and the surfaces of the trunk. The size of these blood lacunae, however, are far less than in *Inopinata inflata* as described by Fenaux and Youngbluth (1991), now known as *Oikopleura inflata* (Fenaux, 1998).

Tail: the tail length is approximately 5 times the trunk length (Fig. 1A). In the largest specimen recovered it was about 5 mm long. From the anterior attachment of the tail, near the posterior margin of the rectum, the dorsal and ven-

tral tail fins widens rapidly to give a total tail width of approximately 1.5 mm, or about twice the width of the trunk. Further back, the tail fins are slightly and gradually reduced in width until the distal segment where they taper off more rapidly to form a smooth terminal curvature. The rim of these fins are smooth and no lateral extensions, like those described for *Mesopelagica caudaornata* by Fenaux and Youngbluth (1991), now known as *Oikopleura caudaornata* (Fenaux, 1998), are present. The muscle bands have a width corresponding to about 1/4 the total tail width and gradually tapers off towards the distal extremity of the tail to which they come very close. Each muscle band is rather thin and few specimens have been obtained with the tail in a satisfactory degree of preservation for detailed study. The notochord has a diameter equal to approximately 1/3 the width of the muscle bands and tapers off and terminates somewhat before the distal extremity of the tail muscles and tail fin.

Subchordal cells: a single row of small plate-like subchordal cells are present between the ventral borders of the bilateral muscle plates in the distal 1/3 of the tail (Fig. 1A and 2D). The row consists of a posterior group of some 8 cells and an anterior group of some 13 cells, separated by a short interval (Fig. 1). The platelike cells are difficult to discern in lateral view without specific staining as their streak-like profile is easily camouflaged by the over- and underlying myofibrils. (In Fig. 2D these cells are squeezed below their normal position by the coverslip compressing the tail).

ETYMOLOGY. - The specific name is dedicated to my dear friend Dr Gabriel Gorsky at Villefranche sur mer for his great contribution to modern appendicularian research and for his willingness to take the coordinator role for the EURAPP project when I was prevented from doing so.

HABITAT. - So far the present species has been identified in low numbers in numerous plankton samples from the depth interval of 1200 to 400 m in Sognefjorden, more rarely in more superficial waters of the same fjord. It has also been found in low numbers throughout the year in Herdlefjorden (bottom depth 270 m at sampled

station). At both stations a temperature of approximately 7.1°C, a salinity of 35.4‰, and an oxygen content of 7 to 8 mg/L prevailed throughout the year below the thermocline. There is also some indication that the species occasionally may be found in more superficial waters (<100m deep) in the coastal archipelag of Western Norway (pers. obs.) and in Korsfjorden, south of Bergen (Martinussen, pers. comm.). The presence of the same species in more open oceanic environment is dubious, as I would expect it to be discovered and described long ago in such a case. The seasonal abundance of the new species need further elucidation, but seems to be fairly even throughout the year.

DISCUSSION

The spacious layout of the posterior trunk segment and small size of the right stomach lobe, as well as the short extension of the oikoblastic epithelium in the posterior direction, with prominent strand-like extensions of this epithelium, as seen in the present species are characteristics rarely seen among oikopleurid appendicularians. Additionally, the number and disposition of the subchordal cells in the tail and the pattern of bioluminescent inclusion bodies in the house rudiment of the present species have never been reported in any known species of Appendicularia. Further the nuclear pattern of the oikoblastic epithelium of the present species deviates in specific details from that of all oikopleurids examined so far.

Hitherto the Oikopleuridae have been classified mostly based on the configuration of their digestive tract (Lohmann, 1933; Bückmann and Kapp 1975; Fenaux 1998). The main reason for this seems to be that the alimentary structures of these extremely fragile animals remain identifiable with more details than most other tissues in standard zooplankton samples. However helpful in practical work, the plain geometry of successive segments of the digestive tract cannot be considered a strong criterium for a natural taxonomic classification. This is particularly true since the more fundamental presence or absence of oral glands, subchordal cells, and probably the presence of bioluminescent inclusion bodies, although difficult to study in detail, are now

characters shared by one subgenus (*Vexillaria* Lohmann, 1933 of the genus *Oikopleura* Mertens, 1830) and two genera (*Folia* Lohmann, 1892 and *Stegosoma* Chun, 1887). These evidently belong to a natural group which should be separated from the subgenus *Coecaria* Lohmann, 1933 of the genus *Oikopleura*. Likewise, the lack of the oral gland/subchordal-cell/inclusion-body triad unifies the subgenus *Coecaria* of genus *Oikopleura* and the genera *Chunopleura* Lohmann, 1914 and *Megalocercus* Chun, 1887 in another natural group. The present species, based on its presence of oral glands, subchordal cells, house rudiment inclusion bodies, and bioluminescent property, evidently belongs to the first of these groups.

Other characteristic features of the present species brings it close to several species within this natural group. The small size of its right stomach lobe is comparable to that found in *Folia gracilis* Lohmann, 1892 and *F. mediterranea* Lohmann, 1892 as well as *Oikopleura caudaornata* (originally described as *Mesopelagica caudaornata* by Fenaux and Youngbluth, 1991), and to some degree in *O. inflata* (originally described as *Inopinata inflata* by the same authors). Likewise, the limited posterior extension of the oikoblastic epithelium in the present species, as well as the strand-like posterior extensions of this epithelium, comes close to the comparable structures in *O. caudaornata* and *O. inflata*. However, *O. caudaornata* has a much more elongated trunk and its tail ornaments and overall size is highly different from those of the present species. Likewise, *O. inflata* has a much wider trunk, narrower tail muscle and its subchordal cells disposed in a pattern clearly distinguishable from that observed in the present species. For the two *Folia* species neither the extent of their oikoblastic epithelium, nor the disposition of their subchordal cells should cause confusion with the present species. Unfortunately, the presence of house rudiment inclusion bodies has not been verified for any of the mentioned *Folia* and *Oikopleura* species, neither has the nuclear pattern of their oikoblastic epithelia been adequately mapped. For future confirmation of a robust differential diagnosis, studies of these elements should be undertaken.

An absolute secure diagnosis of the present species seems possible by examination of the inclusion body pattern in its house rudiments

and mapping of the nuclear pattern of its oikoblastic epithelium. A reservation should here only be made for the unlike future discovery of identical patterns in another species, whose house rudiments and oikoblastic epithelium has yet to be examined (cp. Galt and Flood, 1998).

PHYLOGENETIC RELATIONS

Among approximately 70 species of appendicularia recognized worldwide (Fenaux, 1998) the present species evidently belongs to the family *Oikopleuridae* Lohmann, 1915, subfamily *Oikopleurinae* Lohmann, 1896 and supergenus *Labiata* Fenaux, 1993. Further, as mentioned above, the presence of oral glands and subchordal cells, as well as house rudiment inclusion bodies (with a probable bioluminescent property), are characters unifying the subgenus *Vexillaria* of the genus *Oikopleura*, now containing 11 species (Fenaux, 1998) with two additional genera: *Stegosoma* and *Folia*, containing 3 additional species. Among these the monotypic *Stegosoma magnum* differs markedly from the rest in numerous characters, however, the separation of the two *Folia* species from 11 *Vexillaria* species seems largely artificial to the present author, and the newly discovered species definitely belongs to this group.

Phylogenetic relations within this '*Vexillaria*' group is difficult to suggest based on established knowledge. In addition to the coarser morphology of their trunks, finer details in the number and disposition of their subchordal cells, the nuclear pattern of their oikoblastic epithelia and the pattern of inclusion body on their house rudiments need to be known before this may be done in a meaningful way. At present little more may be said than that the geometry of the stomach lobes brings the present species close to *O. caudaornata* and *O. inflata*, as well as to *Folia gracilis* and *F. mediterranea*. Further, that the inclusion body pattern with lines of variable geometry brings it close to *O. parva* and *O. albicans* (pers. obs.).

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Drs. G. Gorsky and R. Fenaux, Station Zoologique,

Villefranche sur mer, France, for their continued support, and to Prof. H. J. Fyhn and Cand. Sci. Monica M. Martinussen, University of Bergen, for nice collaboration on the Sognefjorden excursions. Financial support from the European Commission (project MAS3-C98-0161), Université Pierre et Marie Curie, Paris, and the Norwegian Research Council (grant no. 131425/410) is highly appreciated.

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Received: January 7, 2000